

PATTERNS OF ASSOCIATION OF SECONDARY SPECIES IN ROOSTS OF EUROPEAN STARLINGS AND COMMON GRACKLES

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Composition of roosting flocks varies from single-species groups to aggregations of many different species. Mixed flocks are often composed of one to three primary species making up the largest proportion of the association, with a variable number of secondary species making up the remainder (Gadgil 1972). Questions relating to the functional significance of communal roosting behavior have been a major focus of recent research (e.g., de Groot 1980, Loman and Tamm 1980, White 1980, Fleming 1981, Weatherhead 1983). However, the role of secondary species in these flocks has received little attention.

Roost studies have generally emphasized primary species, often with observations of secondary species reported only incidentally. Many of the resulting data are incomplete and few are quantified. Also, most studies have emphasized individual roosts and generally have not lasted throughout roosting seasons. For example, Meanley (1965, 1971) did extensive work in the southern U.S. on the biology of blackbird roosts, but provided little information on secondary species. Similarly, Robertson et al. (1978) provided some quantitative information, but most data on secondary species were collected in a single day during 3 man-hours of walks near a large winter roost. Gadgil (1972) discussed the role of mixed roosts, but provided no quantified observations (Gadgil and Ali 1976).

In addressing the question of why mixed-species roosting flocks form, Ward and Zahavi (1973:524) said, "We have not personally found any situations where two or more species with completely dissimilar foods or feeding places form mixed roosts—except where this can be explained in terms of a shortage of suitable roost sites." They later summarized the situations where mixed species roosts may be formed: (a) limited availability of roost sites; (b) where one species selects the communal roost of another species as a safe site (predator protection) for its own communal roost; (c) species with similar foraging requirements roost together in order to share information. Situations (a) and (b) are exceptions to what was otherwise offered as a general explanation for roosting behavior (situation [c]—the information exchange hypothesis).

We believe the apparent conformity of mixed flocks to these situations is largely due to the scant data on secondary species. In this study our main goal was to examine Ward and Zahavi's (1973) prediction that mixed

species roosting flocks generally (allowing for exceptions [a] and [b] above) contain only species with similar feeding requirements. We hypothesized that (1) some secondary species would show consistent patterns of association in many roosts and over long periods while being sufficiently distinct in their foraging requirements so as to preclude benefits from information exchange; and (2) population sizes of some secondary species would be large enough (Pulliam 1973) to provide maximum levels of predator protection without need to further increase flock size by roosting with other species. We did not consider limited availability of roost sites, because earlier studies suggested that this was unlikely in our study area (Lyon and Caccamise 1981, Caccamise et al. 1983). Support for our hypotheses would suggest that information exchange (Ward and Zahavi 1973) alone does not explain aggregation of mixed species into roosting flocks, and that alternative or additional factors are important in their formation.

We examined patterns of association for secondary species in roosts where primary species were European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*). Our approach was to (1) identify secondary species present in all roosting flocks over a large study area; (2) determine seasonal pattern of association for each species within the regional roosting population; and (3) examine the distribution of secondary species among individual roosting flocks on a regional basis.

STUDY SITE AND METHODS

Data collection for secondary species took place during local roosting seasons (June–Nov.) of 1979 and 1980; however, studies of primary species extended from 1977–82 (Caccamise et al. 1983). A region within the piedmont and inner-coastal plain provinces of central New Jersey (Robichaud and Buell 1973) was searched rigorously for all roosts containing at least 2000 birds. Roosting assemblages were located throughout the roosting season by regularly traveling surveillance routes in the evening. Flight lines were identified and followed to roost sites.

The census area included approximately 1000 km² (Caccamise et al. 1983). Size was defined initially (1977) by the limits of our ability to conduct thorough censuses. Once the distribution of roosts was determined, we confined our searching to within the perimeter established by peripheral roost sites. To count birds, one to four observers were stationed at roosts where major flight lines could be viewed during evening arrivals or morning departures. Birds were counted by species in 5-min intervals. Counts taken during inclement weather were not included in estimates of population sizes, as roosting activity was erratic at these times. Total population sizes over the census area were based on 100 counts in 1979 and 113 in 1980. Population sizes were estimated at 5-day intervals by summing number of individuals of each species present in each active roost.

RESULTS

There were 24 active roosts within the census area in 1979 and 18 in 1980. Individual roosts were active from 3 to 20 weeks and ranged in

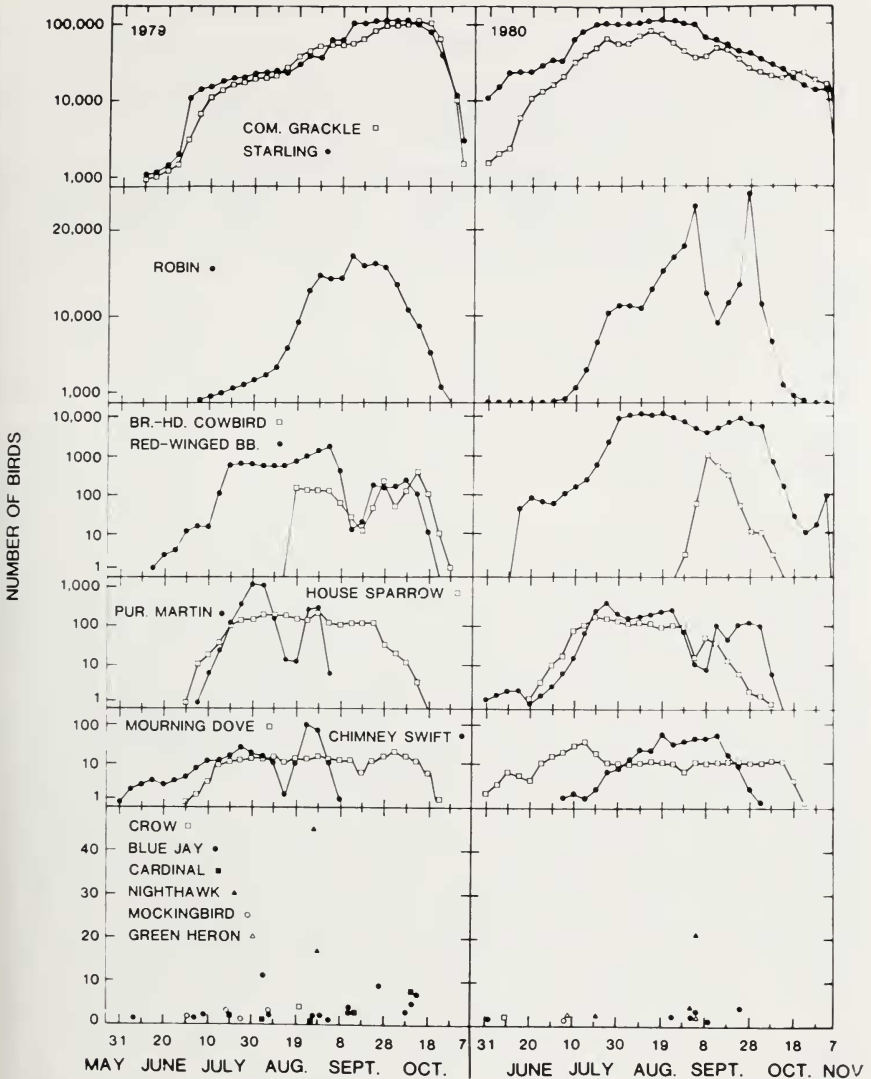


FIG. 1. Number of birds by species in all active roosts in the study area (abbreviations: starling—European Starling; com. grackle—Common Grackle; robin—American Robin; br.-hd. cowbird—Brown-headed Cowbird; red-winged bb.—Red-winged Blackbird; pur. martin—Purple Martin; cardinal—Northern Cardinal; nighthawk—Common Nighthawk; mockingbird—Northern Mockingbird; green heron—Green-backed Heron).

TABLE 1

NUMBER OF ROOSTS WHERE EACH SPECIES WAS RECORDED DURING THE 1979 AND 1980 SEASONS. TOTAL NUMBER OF ROOSTS ACTIVE AT EACH DATE IS EQUAL TO THE NUMBER RECORDED UNDER STARLINGS AND COMMON GRACKLES

Date	Number of roosts occupied by roosting species*																
	Star. grack.		Robin		Br.-h. cowbrd.		Red-wng. blkbd.		Pur. mart.		House sprw.		Chimney swift		Mourn. dove		
	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	
10 June	1	3								1				2		2	
15 June	1	5					1	1		1				2		2	
20 June	2	5					1	1		1		2		1		3	
25 June	2	6		1			2	2		1		2		1		4	
30 June	5	7		1			3	3		1		1	3	1		1	6
5 July	10	8	4	5			4	4	1	1	3	4	2	1	2	2	8
10 July	13	10	9	9			4	5	3	2	5	7	3	1	2	6	6
15 July	14	13	10	13			6	7	3	3	8	7	4	1	4	6	6
20 July	14	15	11	14			8	10	3	4	9	9	6	2	5	6	6
25 July	14	15	12	14			8	11	3	4	9	9	8	1	5	7	7
30 July	13	15	11	14			8	9	5	4	10	9	7	2	7	4	4
4 Aug.	13	15	11	14			6	6	5	4	10	8	5	3	6	5	5
9 Aug.	15	13	14	12			6	8	5	4	10	6	4	5	5	3	3
14 Aug.	16	13	15	12			5	8	5	4	9	7	3	7	4	3	3
19 Aug.	16	13	14	12	1		2	6	3	5	8	7	2	9	6	4	4
24 Aug.	15	13	14	12	1		2	6	3	5	9	7	3	9	6	6	6
29 Aug.	14	14	13	13	1	1	2	6	2	4	8	6	3	9	7	4	4
3 Sept.	14	13	13	12	1	2	1	6	1	3	7	4	3	6	8	3	3
8 Sept.	11	11	11	10	1	2	1	3	1	6	5	2	3	6	3	6	3
13 Sept.	10	11	10	10	2	2	2	5	2	6	2	0	2	5	2	2	2
18 Sept.	10	11	10	10	2	2	1	5	2	5	1		2	3	3	3	3
23 Sept.	10	11	10	10	2	2	2	6	2	3	1		2	4	4	4	4
28 Sept.	9	11	10	10	3	2	2	6	1	2	1		2	5	2	2	2
3 Oct.	9	11	10	10	3	1	2	5	1	2	1		1	5	3	3	3
8 Oct.	8	10	8	9	2	1	2	5	1	1	1			5	3	3	3
13 Oct.	7	9	7	9	2		2	3			1			3	3	3	3
18 Oct.	7	6	6	6	2		2	2						2	2	2	2
23 Oct.	6	5	4	5	1			2						1	1	1	1
28 Oct.	2	2		2	1			1									
2 Nov.	1	2		2													

* Star. grack.—European Starling and Common Grackle; Br.-h. cowbrd.—Brown-headed Cowbird; Red-wng. blkbd.—Red-winged Blackbird; Pur. mart.—Purple Martin; House sprw.—House Sparrow; Mourn. dove—Mourning Dove.

size from 2000 to more than 100,000 birds. The most abundant species in roosts were European Starlings and Common Grackles (Fig. 1). Secondary species, while present at varying times during the roosting season, constituted relatively small proportions of the total roosting population.

Population sizes for all species were very similar in both years, as were dates when secondary species were present in roosts (Fig. 1). In both years, the roosting season began in early June. In 1979 it built to a peak on 8 Sept., while in 1980 the peak occurred about a month earlier (19 Aug.). In both years, number of active roosts increased through the first half of the season and peaked at about the same time as population size (Table 1). Afterwards, population size and number of active roosts declined through the end of the local roosting season (Caccamise et al. 1983).

American Robins (*Turdus migratorius*) were the most abundant secondary species (Fig. 1), with juveniles forming a large and conspicuous part of all robin flocks that we encountered. In 1980 the number of robins declined markedly during late Aug. and early Sept. (Fig. 1). This coincided with a period of severe drought in the census area (N.O.A.A. 1980). A similar decline occurred for primary species, but, unlike starlings and grackles, numbers of robins present in roosts increased again soon after the first significant rainfall (17 Sept.).

Except for very early in the season, robins were present in nearly every active roost (Table 1). Maximum flock sizes for robins were as large as 20,000 (Fig. 2). Of the 40 roosts (both years) where robins were present, maximum flock sizes were usually larger than 100 (7 held >2000 robins, 6 held 1000–2000, 13 held 500–1000, 7 held 100–500, 8 held <100).

Red-winged Blackbirds (*Agelaius phoeniceus*) and Mourning Doves (*Zenaida macroura*), like robins, were also present for much of the season (Table 1). Their numbers were much lower, however, and they were present in fewer active roosts (Table 1, Fig. 2). We found examples of roosting flocks where each of these species (robin, red-wing, dove) was the primary species. Red-wings were primary species at two roosts in stands of common reed (*Phragmites communis*) along water courses within the study area. At one site where robins were numerous, they became the primary species when the roost was abandoned by starlings and grackles. We did not follow their activity after starlings and grackles left, but the population was clearly declining (Fig. 2, 1979, Roost 19).

The remaining secondary species were less widely distributed among roosts (Fig. 2). Flocks tended to be concentrated at a few sites, where they remained for relatively short intervals. For example, Brown-headed Cowbirds (*Molothrus ater*) occurred in only three roosts in 1979 and two in 1980 (Table 1, Fig. 2), but they were present in the study area over similar dates both years (Fig. 1).

Counts for Purple Martins (*Progne subis*) and House Sparrows (*Passer domesticus*) each included a small percentage (<10%) of Tree Swallows (*Tachycineta bicolor*) and House Finches (*Carpodacus mexicanus*), respectively. These data were combined, as we felt identifications were likely

unreliable given the poor light conditions and the often high rates of arrival for primary species.

Chimney Swifts (*Chaetura pelagica*) generally circled high over roost sites. They appeared specifically oriented to the sites, and were not simply present in the area. They apparently entered roosts, as we caught one in a mist net within the canopy of the roost vegetation (Lyon and Caccamise 1981).

Several secondary species were relatively uncommon (Fig. 1, bottom). Species like Green-backed Heron (*Butorides striatus*), Northern Mockingbird (*Mimus polyglottos*), and Northern Cardinal (*Cardinalis cardinalis*) were probably residents of woodlots where roosts were located. Although the American Crow (*Corvus brachyrhynchos*) is notorious for large roosting flocks, their numbers were always quite low in our roosts. In many areas Common Nighthawks (*Chordeiles minor*) begin migration as early as mid-Aug. (Selander 1954), which was when they appeared in our roosts during both years of the study.

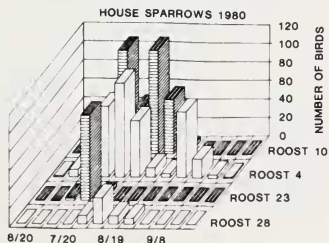
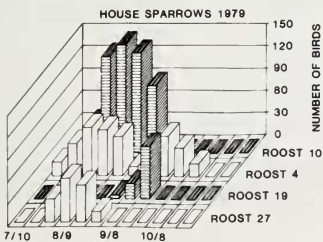
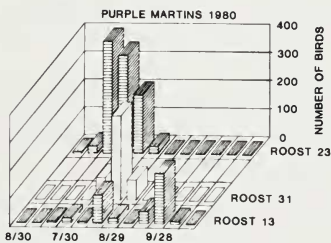
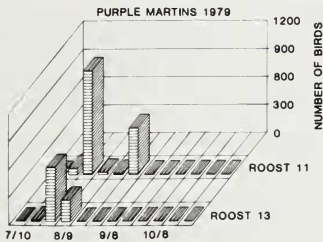
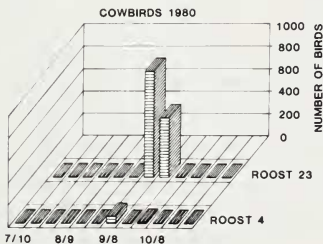
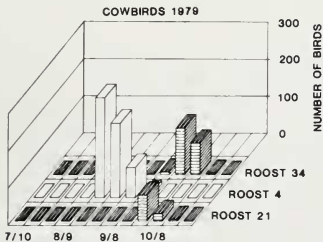
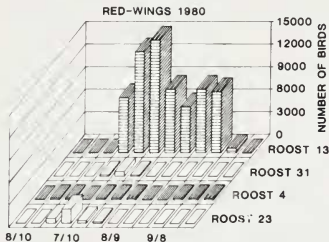
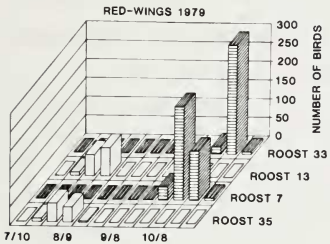
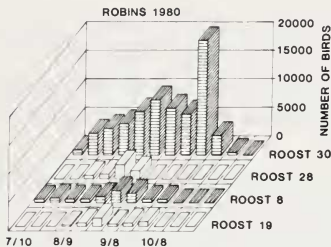
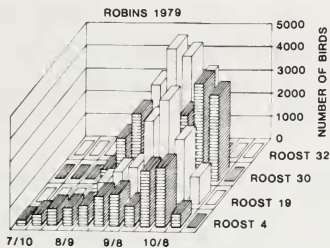
DISCUSSION

Secondary species can be overlooked easily when roosting populations are large and primary species are conspicuous. We found secondary species, however, in nearly every roost examined. This was true throughout the season and for all roost sizes. Although each species had a unique pattern of association, their presence together resulted in considerable heterogeneity in species composition throughout the roosting season.

In presenting the information center hypothesis, Ward and Zahavi (1973) were unable to find any evidence that mixed species roosting flocks included species with dissimilar foods or feeding places, except where roost sites were limited. By providing support for our first hypothesis, we have shown that this was not the case in our study area. Many secondary species have foraging requirements quite distinct from other species in the roosts. For these, interspecific exchange of foraging information appears an unlikely reason to form mixed species roosting flocks (e.g., House Sparrows, Mourning Doves, Red-winged Blackbirds, and Purple Martins).

For other species, determining the potential for interspecific exchange of foraging information is more difficult (e.g., grackles and starlings). This is because we do not know how similar foraging requirements must be in order for foraging benefits to be possible. For example, in our study

FIG. 2. Seasonal patterns in roosting flock size at individual roosts. Roosts depicted for each secondary species were those with the largest population sizes.



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area Common Grackles occurred in less than 10% of starling foraging flocks observed over a period of 17 months (Fischl 1983). It is open to conjecture whether or not foraging requirements of these species are sufficiently distinct to preclude foraging benefits as a basis for mixed species roosting.

In our second hypothesis we predicted that, for some species, numbers of individuals in roosting flocks were sufficiently large to maximize predator protection (e.g., Lack 1968, Gadgil and Ali 1976) without the need to form mixed species flocks. Pulliam (1973) pointed out that relationships between levels of predator protection and group size are likely asymptotic, with maximum benefits achieved at relatively small group sizes (<100). In addition, costs increase with flock size because of increased commuting distances and greater competition for favored positions at both roost sites (Swingland 1977) and in foraging areas (Hamilton and Gilbert 1969).

In our study, size of single-species aggregations (within mixed roosting flocks) varied greatly among roosts (Fig. 2). The more abundant species (e.g., robins) occurred in large numbers at active roosts throughout the study area. For these species aggregations were much larger than the minimum size required for maximizing predator protection. Flock sizes for less abundant species (e.g., Purple Martins, House Sparrows) also were often large enough to maximize predator protection, because they aggregated at few sites generally forming relatively large roosting flocks. Thus, for most secondary species, predator protection alone does not appear to explain the formation of mixed species roosting flocks.

Many factors likely influence an individual's choice of a night time roosting site. Our results, however, lead to the conclusion that neither limited availability of roost sites (Caccamise et al. 1983) nor information exchange (Ward and Zahavi 1973) offer suitable explanations for the presence of some species in our roosting flocks. Also, it appears, on theoretical grounds (Pulliam 1973), that predation protection does not alone offer a satisfactory explanation.

The security offered by roosting sites certainly must be an important part of the site selection process. Protection from predators, however, is only one of many factors influencing the security and overall quality of roost sites. Individuals must select sites based on many features, including absence from disturbance, protection from weather events, and proximity to feeding areas. Typically, roosting activity begins with a small group, which increases in size over periods ranging from days to months, with individual sites often used for many years (Caccamise et al. 1983). Therefore, the factors influencing site quality appear to be generally stable over time.

An individual or group seeking a roost site can avoid risks of making a poor selection by choosing to roost at an established site. This feature might be particularly important to young of the year or transients moving through an area. Both groups would be unfamiliar with local conditions and could benefit by selecting a site of established quality. In this way active sites would attract individuals of many species because they are secure and provide some assurance that at least minimum requirements will be met. This could lead to development of very large roosting flocks made up of species having little apparent basis for commonality (e.g., Common Nighthawks, Brown-headed Cowbirds).

This concept broadens the conventional view of predator protection by considering the importance of (1) risks from a variety of sources; and (2) overall quality of roost sites. It also provides an explanation—at least in part—for why roosts are often large and contain a variety of different species. Minimizing risks associated with the selection of roost sites, however, does not offer an explanation for why roosts form in the first place.

SUMMARY

This study examines population dynamics of secondary species associated with roosts composed primarily of European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*). Our goal was to determine patterns of association for secondary species and to evaluate the role of interspecific relationships in roosting flocks. We estimated sizes of roosting populations over 2 seasons for all roosts within a large census area. From June to November roosts were active 3–20 weeks and varied in size from 2000 to over 100,000 individuals. We found 17 secondary species; numbers ranged from fewer than 10 individuals (Green-backed Heron, *Butorides striatus*) to over 20,000 (American Robin, *Turdus migratorius*). They were in nearly every roost, irrespective of season or roost size. Although each species had a unique pattern of association, their presence together resulted in considerable species heterogeneity.

For those roosting species with distinct foraging requirements, interspecific exchange of foraging information is an unlikely reason to form mixed species roosting flocks. Also, species that form large (>100) roosting flocks apparently do not join mixed species flocks only for added predator protection, as these benefits are likely asymptotic at relatively small flock sizes. There are many factors that make roost sites attractive. By selecting occupied roosts, individuals can lower the risk of choosing poor sites, and be assured that, at least, minimum requirements will be met. This concept provides an explanation for why very large roosting flocks develop, and why they are often composed of species with little apparent basis of commonality.

ACKNOWLEDGMENTS

For their contributions to field work we thank N. Bent, D. Brook, A. Conroy, C. Cove, C. Kopec-Korsmo, P. McIsaac, and R. Unnasch. D. Morrison provided valuable suggestions on an earlier draft of the manuscript. This is New Jersey Agricultural Experiment Station Publication No. D-08230-26-83, supported by State Funds and U.S.D.A. Regional Research Funds.

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